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Scaling of the extrastriate neural response to symmetry

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ABSTRACT

Neuroimaging work has shown that visual symmetry activates extrastriate brain areas, most consistently the lateral occipital complex (LOC). LOC activation increases with proportion of symmetrical dots (pSymm) in a degraded display. In the current work, we recorded a posterior ERP called the sustained posterior negativity (SPN), which is relatively negative for symmetrical compared to random patterns. We predicted that SPN would also scale with pSymm, because it is probably generated by the LOC. Twenty-four participants viewed dot patterns with different levels of regularity: 0% regularity (full random configuration) 20%, 40%, 60%, 80%, and 100% (full reflection symmetry). Participants judged if the pattern contained "some regularity" or "no regularity". As expected, the SPN amplitude increased with pSymm, while the latency and duration was the same in all conditions. The SPN was independent of the participant's decision, and it was present on some trials where people reported 'no-regularity'. We conclude that the SPN is generated at an intermediate stage of visual processing, probably in the LOC, where perceptual goodness is represented. This comes after initial visual analysis, but before subsequent decision stages, which apply a threshold to the analog LOC response.
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1. Introduction

Symmetry is relevant for a variety of visual processes, such as for perceptual grouping and pattern recognition (Machilsen, Pauwels, & Wagemans, 2009), face recognition and for discriminating living organisms from non-living objects (Tyler, 1995). Psychophysical work has shown that reflection on the vertical axis is more salient than when the axis is horizontal or oblique (Bertamini, Friedenberg, & Kubovy, 1997) and that reflection detection is superior to translation and rotation (Royer, 1981). Symmetry discrimination is not an all or nothing affair: people can discriminate regularity in noisy displays (Barlow & Reeves, 1979). It is also well known that humans and animals like symmetry, whether it is a property of abstract patterns (Eysenk, 1941; Jacobsen & Höfel, 2002; Makin, Pecchinenda, & Bertamini, 2012) or potential mates (Bertamini, Byrne, & Bennett, 2013; Grammer, Fink, Møller, & Thornhill, 2003; Rhodes, Proffitt, Grady, & Sumich, 1998). Despite the perceptual and emotional relevance of symmetry, its neural basis is still under investigation.

There are many ways of classifying regular patterns, including Euclidian plane isometries, the 7 frieze groups and the 17 wallpaper groups (Grunbaum & Shephard, 1987). Here we focus on the neural response to reflectional symmetry. The extent to which these results generalize is a topic for future work.

1.1. Brain responses for symmetry

The existing neuroimaging work symmetry perception was reviewed by Bertamini and Makin (2014). Functional magnetic resonance (fMRI) and Trans-cranial Magnetic Stimulation (TMS) studies have revealed that the lateral occipital complex (LOC) is causally involved in symmetry detection (Bona, Herbert, Toneatto, Silvanto, & Cattaneo, 2014; Cattaneo, Mattavelli, Papagno, Herbert, & Silvanto, 2011; Sasaki, Vanduffel, Knutsen, Tyler, & Tootell, 2005). Sasaki et al. (2005) recorded cerebral blood flow with fMRI while participants viewed reflection or random dot configurations. The authors found that V3A, V4, V7 and the LOC were more activated for reflection. There was no response to reflection in V1 and V2. Importantly, the activity within this extrastriate network was positively correlated with subjective perception of symmetry: the more the stimuli were perceived as symmetrical, the more they evoked neural activity. Furthermore, the proportion of symmetrical and random dots in the displays was varied, both the probability of reporting symmetry and size of the neural response increases with this variable. We refer the proportion of symmetrically positioned dots in a pattern as 'pSymm'.

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There have also been several ERP studies on symmetry perception. First, Norcia, Candy, Pettet, Vildavski, and Tyler (2002) found that amplitude was reduced for symmetrical compared random pattern in posterior electrodes from around 220 ms onwards. Jacobsen and Höfel (2003) reported a similar sustained posterior negativity (SPN) beginning after the P1 and N1 components of the visual evoked potential at posterior channels. The SPN is a *difference wave* – the term 'negative' refers to the fact that the amplitude was more negative for the symmetrical than random patterns. The SPN is partially independent of task, it can be recorded when participants are not explicitly classifying patterns as symmetrical or random (Höfel & Jacobsen, 2007a) or when people deliberately misreport their responses (Höfel & Jacobsen, 2007b) but can be reduced if people are attending to superimposed words instead of the symmetry of the patterns (Rampone, Makin, & Bertamini, 2014).

Makin, Rampone, Pecchinenda, and Bertamini (2013) showed that the SPN is larger for reflection than translation and rotation symmetry, and concluded that reflection is the optimal stimulus for a more general regularity-sensitive network in the extrastriate visual cortex. Other experiments have found that the SPN is similar for symmetrical objects and gaps between objects (Makin, Rampone, Wright, Martinovic, & Bertamini, 2014) and that the SPN is a view-invariant response to symmetry when participants are attending to regularity (Makin, Rampone, & Bertamini, 2015). The SPN is similar for horizontal and vertically oriented patterns (Wright, Makin, & Bertamini, 2015).

These studies tell us much about symmetry networks in the brain, but they do not clarify whether the SPN wave is generated by the LOC, identified as the major 'symmetry region' by Sasaki et al. (2005), Tyler et al. (2005), Cattaneo et al. (2011) and Bona et al. (2014). Makin et al. (2012) did perform a preliminary source localization analysis that identified SPN generators in lateralized posterior brain regions. However, this was not precise enough to warrant a strong conclusion.

1.2. Current work

We presented abstract patterns while recording EEG. The patterns varied in terms of the proportion of reflection over random elements. There were 300 random trials, and 60 trials with 20%, 40%, 60%, 80% and 100% symmetry (Figs. 1 and 2). We refer to this factor as 'pSymm'. On every trial, participants were forced to choose a response, either "some regularity" or "no regularity". For all 5 levels of pSymm, the SPN was calculated as the difference from the random wave.

Sasaki et al. (2005) found that the BOLD response in LOC and V4 parametrically increased with the proportion of reflected dots. If they SPN is generated by symmetry related activity in these areas, it will also scale with pSymm. This is important purely in terms of understanding the nature of the SPN signal. However, a positive result would also tell us something about the nature of symmetry processing in the extrastriate visual cortex. A parametric increase in the BOLD response is not conclusive: Increased BOLD could be produced by a longer-lasting period of symmetry related activity or by an earlier onset of the symmetry response. Alternatively, the temporal characteristics of the response could be the same for all levels of pSymm, but the amplitude response could increase with pSymm. The SPN has the temporal resolution to distinguish between these distinct 'amplitude' and 'duration' possibilities.

The second aim of the current study was to characterize the relationship between the neural response to symmetry in the extrastriate cortex and higher decision-making processes in the brain. Consider the trials with a medium pSymm, say 60% and 40%. Participants sometimes correctly reported 'some regularity' (a hit) and sometimes erroneously reported 'no regularity' (a miss). If the SPN is generated by the decision stage, there should be no SPN whatsoever on the miss trials, and a large, similar SPN on all the hit trials. Conversely, it could be that the SPN reflects an analog response to symmetry, at an intermediate level of the processing hierarchy. A subsequent decision stage applies a threshold to this signal. In this case, we will still record an SPN, albeit at a lower amplitude, on the miss trials.

These two questions represent a major step forward in understanding the neural basis of symmetry perception. The current work tests whether pSymm alters the amplitude or duration of the neural response in extrastriate symmetry networks, and also how these networks fit into the rest of cognitive processing. More generally, this is an important topic for understanding mid level vision, where consciously experienced visual structure emerges (Peirce, 2014).

2. Method

2.1. Participants

Twenty-four participants took part in the experiment (age range: 19–46, average age 21.5 years, 9 males, 5 left handed). All participants had normal or corrected to normal vision. They provided a written consent for taking part and received course credits. The experiment was approved by the Ethics Committee of the University of Liverpool and was conducted in accordance with the Declaration of Helsinki.

2.2. Apparatus

Apparatus was identical to that used in previous SPN studies (e.g. Makin et al., 2012). Participants sat 140 cm from a

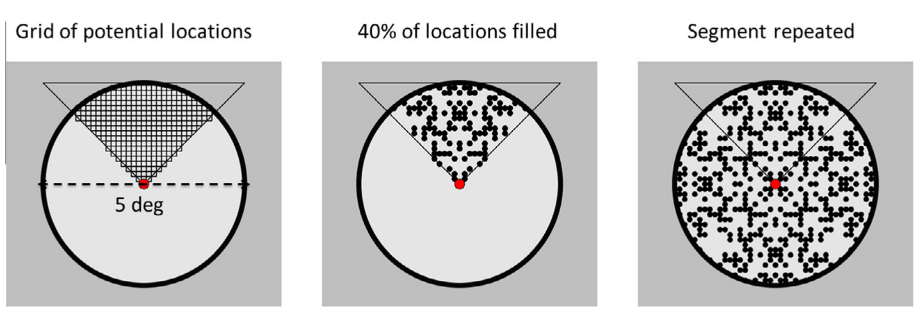

Fig. 1. Stages in construction of 100% symmetry. This does not show the stimuli as seen by the participants, but illustrates the steps involved in construction. First a single tiled segment was produced, then 40% of the cells were occupied with a dot in a reflectional configuration. This segment was replicated in the other three orientations, giving fourfold symmetry. For random trials, there was no reflection and each segment was generated independently. For trials with an intermediate level of symmetry, the symmetrical dots were repeated in each segment, but the randomly positioned dots were generated afresh each segment.

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